Fungi from Canadian coniferous forest soils

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The fungus flora from four pine forest soils was investigated. Qualitative studies used a soil-washing method, whereas quantitative investigations were performed using a direct observation technique. Results indicate that the fungus populations on litter and humus from all four forest soils are fairly similar, with *Cladosporium herbarum*, *Aureobasidium pullulans*, *Alternaria* sp., and various members of the order Sphaeropsidales being common in the litter, and *Trichoderma* and *Penicillium* species increasing in frequency in the F and H layers. The fungi isolated from the mineral soil horizons were more varied in nature, but certain genera seemed to be found frequently; these included *Mortierella*, *Chrysosporium*, *Oidiodendron*, *Paecilomyces*, *Cylindrocarpon*, *Torulomyces*, and sterile dark fungi.

A detailed investigation of a *Pinus strobus* forest at St. Williams, Ontario, revealed no distinct seasonal patterns in the relative frequencies of the species of fungi.

Quantitative studies showed that, in all soils, mycelial content decreased with depth from the humus. A comparison of the four sites showed a wide variation in fungal mycelium, varying from 30 m/g dry soil under *Pinus strobus* (in the A_1 horizon) to 1540 m/g under *P. contorta* during May. Seasonal data from the *P. strobus* forest indicate a peak in mycelial content during August.

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Les auteurs ont étudié la flore fongique du sol de quatre pinèdes. Les études quantitatives faisaient appel à une méthode par délavage du sol, alors que les examens quantitatifs ont été réalisés à l'aide d'une technique d'observation directe. Les résultats indiquent que les populations fongiques sur la litière et l'humus des quatre sols forestiers sont à peu près semblables; *Cladosporium herbarum*, *Aureobasidium pullulans*, *Alternaria* sp. et différents membres de l'ordre des Sphaeropsidales étaient fréquents dans la litière, et des espèces de *Trichoderma* et de *Penicillium* augmentaient en fréquence dans les horizons F et H. Les champignons isolés des horizons minéraux du sol étaient de nature plus variée mais certains genres semblaient fréquents; ceux-ci comprennent *Mortierella*, *Chrysosporium*, *Oidiodendron*, *Paecilomyces*, *Cylindrocarpon*, *Torulomyces* et des champignons stériles à mycélium foncé.

Une recherche méticuleuse dans une forêt de *Pinus strobus* situé à St. Williams en Ontario n'a montré aucun patron saisonnier clair dans les fréquences relatives des espèces de champignons.

Les études quantitatives ont montré que, dans tous les sols, le contenu en mycélium décroit avec la profondeur à partir de l'humus. Une comparaison des quatre sites a montré beaucoup de variation dans le mycélium fongique, qui passait de 30 m/g de sol sec sous le *Pinus strobus* (dans l'horizon A_1) à 1540 m/g sous le *P. contorta* au mois de mai. Des données saisonnières obtenues dans la forêt de *P. strobus* montrent un pic dans le contenu en mycélium en août. [Traduit par le journal]

Introduction

Although there have been many publications on the fungi of forest soils, many have been little more than species lists, based on data from either the dilution plate or the soil plate method. These reports, though they provide valuable taxonomic data, do not give any information on the distribution of fungi at the microhabitat level, or their relationship with the environment in which they live.

Two comprehensive surveys of the fungus flora of coniferous forest soils have been reported, one on a podzol soil under *Pinus sylvestris* in England (Kendrick and Burges 1962; Williams 1963; Williams and Parkinson 1964), and the other on recolonized sand dunes under *Pinus nigra* (Parkinson and Balasooriya 1967). In both these studies fungi were isolated separately from the different soil horizons, from the freshly fallen litter through to the C horizon of the mineral soil, using the soil-washing technique of Parkinson and Williams (1961) as the major method of isolation. There have also been a number of studies concerned with the decomposition of litter from various tree species. These include the studies of Hayes (1965*a*, 1965*b*) and Brandsberg (1969), who worked with coniferous trees; Saito (1956) and Hering (1965), who studied the decomposition of deciduous tree litter; and Butcher (1968), who provided data on the decomposition of heartwood of *Pinus radiata* by microfungi.

An examination of the literature on fungi from coniferous forest soils in Canada reveals that

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since the early work of Bisby *et al.* (1933, 1935) the only published reports have been those of Reddy and Knowles (1965), Morrall and Vanterpool (1968), and Bhatt (1970). Of these papers Bhatt's (1970) is a taxonomic survey of the fungi of cedar swamps, and that of Morrall and Vanterpool (1968) is an ecological survey of the boreal forest area, based on dilution plate data from the A_1 horizons only. The study of Reddy and Knowles (1965), however, describes fungal populations on the litter of black spruce (*Picea mariana*), using the soil-washing technique, but is based on one sampling, and therefore does not take seasonal fluctuations of the mycoflora into account.

Because of the very limited knowledge of soil fungi from Canadian forest soils, the study reported here was undertaken as a precursor to studies on the effects of various ecosystem manipulations on soil fungi. The aim of the work was to examine in detail, both qualitatively and quantitatively, the distribution of fungi in the soil profiles of a number of coniferous forest sites and to obtain data on seasonal fluctuations in forest soil mycofloras in a limited number of these sites.

Description of Study Areas

(a) St. Williams

This site is situated at the Province of Ontario Department of Forestry's tree nursery at St. Williams, Ontario. The site is close to Lake Erie and consists of a pure stand of *Pinus strobus* L. about 40 years old, growing on recolonized sand dunes. The sandy soil shows some evidence of leaching in the profile, but being immature, the boundaries of the horizons are not distinct. The horizons are as follows: (1) A_0: 2.5 cm deep, divisible into L, F_1, F_2, and H layers on the basis of the stage of decomposition of the organic materials; (2) A_1: sand, stained dark brown with humus, about 2.5 cm deep; (3) A_2: light greyish in color, 20 cm deep, apparently leached sand; and (4) C: yellowish in color, appearing to be unaltered dune sand.

(b) Kananaskis

The site is situated in the Kananaskis valley, in the Rocky Mountains of southern Alberta, about 60 mi west of Calgary. The site consists of a stand of *Pinus contorta* Dougl. which developed as a result of a forest fire that swept through the valley 35–40 years ago, destroying the spruce trees (hybrids of *Picea glauca* (Moench) Voss and *P. engelmannii* Parry); spruce trees still stand at higher altitudes. The occasional spruce which survived this fire is found on the study area, along with some spruce seedlings which are starting to establish themselves.

The soil is poorly developed, consisting of a sandy deposit on top of river gravel, rarely reaching a depth greater than 50 cm. Defining soil horizons was difficult, but, for convenience, the horizons can be described as follows: (1) A_0: 5 cm deep, divided into L, F_1, F_2, and H layers in the same fashion as was the A_0 horizon at St. Williams; (2) A_1: 2.5 cm deep, irregular in its occurrence. Sand stained dark brown with organic matter; (3) A_2: dark grey sand, about 5 cm deep; (4) B: irregular brown-stained layer of soil 2–3 cm in depth; and (5) C: light-grey sandy material with gravel underneath. The C horizon varied in depth considerably because the gravel was often almost immediately beneath the B horizon.

(c) Petawawa

This site is situated at the Canada Department of Forestry, Petawawa Forest Experimental Station, Chalk River, Ontario, in the Ottawa River Valley, 120 mi north of Ottawa. Samples were received from two sites, one a mixed stand of *Pinus resinosa* Ait and *P. strobus*, and the other a pure stand of *P. banksiana* Lamb. Both sites consisted of sandy soils which are podzolic in nature. The soils of the area have been described by Rennie (1966).

Soil pH

Soil pH was determined with a glass electrode, using a paste of the soil, moistened with distilled water. Four replicate samples were taken from each horizon from Kananaskis and St. Williams. The pH's for the Petawawa soils are those given by Rennie (personal communication). The acidities of the four soils are compared in Table 1. It can be seen that the pH's of the H horizons of the two Petawawa sites are very acidic, 3.9 and 4.5, but are slightly higher in the mineral horizons. The site at St. Williams is slightly acid, being 5.1 in the H horizon and 6.6 in the mineral soil, but the Kananaskis soils are only very slightly acidic (6.8) in the H, and slightly alkaline (7.6) in the mineral horizons.

Methods

Sampling

(1) A_0 Horizon

Samples of the L, F_1, and F_2 layers were collected carefully by hand to minimize contamination with material from the other layers. Samples from each layer were then placed separately in clean polyethylene bags. Samples from the H layer were then removed from the upper mineral soil horizon, using a clean spade, and placed in clean polyethylene bags.

(2) Mineral Horizons

Samples of mineral soil were collected after the removal of the A_0 horizon. A pit, about 45 cm square, was dug down to the C horizon. Samples of mineral soil were removed with a clean trowel from the middle of each recognizable horizon, and placed separately in clean polyethylene bags.

Whenever possible, samples of soil were taken immediately to the laboratory and stored overnight at 2–3°C. Analyses were performed on the samples the next day, thus avoiding excessive storage time. The samples from Petawawa, however, were sent by air, necessitating a delay of 4 days between sampling and processing.

Estimation of Fungal Populations

(1) Qualitative Studies

The method used in this study for isolation and identification of fungi in the soil was the soil-washing method. This technique was used as it allows for the isolation of those fungi growing actively in the soil, rather than those fungi present as spores, which represent past, rather than present, activity. The washing method for the H and F_1 pine needles differed from that used for the other soil layers and will be discussed separately.

(i) L and F_1 layer needles—To wash the L and F_1 needles, the method first described by Kendrick and Burges (1962) and later used by Balasooriya and Parkinson (1967) was used. Five needles from the L and F_1 horizons were placed separately into each of three McCartney vials; thus a total of 15 needles from each layer was used. Twenty milliliters of sterile water was placed in each vial, the caps screwed on, and the vials placed on a reciprocating shaker. The vials were shaken for 2 min at 250 oscillations per minute, after which they were removed, the water decanted off, and the process repeated as many times as necessary. Washing efficiency tests, as described by Kendrick and Burges (1962), showed that it was necessary to wash the L layer needles 10 times and the F_1 needles 20 times to remove the spores from the surface of the needles; these numbers of washings were used in all the work described here. After they were washed, the needles were removed and placed in sterile petri dishes containing filter papers, and allowed to dry for 24 h to reduce bacterial development. When dry, the needles were cut into segments about 2 mm long and two segments placed on each of 50 plates of Czapek-Dox agar, pH 4.5. A sample of 100 needle segments from each layer was thus plated at each sampling time. The plates were incubated at room temperature for 2 weeks and the fungi developing from each particle recorded.

(ii) F_2, H, and mineral horizons—To wash the F_2, H, and mineral soils, a soil-washing apparatus similar to that of Parkinson and Williams (1961) was used. Two and one-half grams of F_2 and H layer material and 5 g of each mineral horizon soil were weighed and placed into separate boxes of the apparatus. The washing boxes were then connected to the sterile water tank and a sterile compressed air source and 50 ml of sterile water was run into each box. The compressed air was then turned on and the soil agitated for 2 min, after which the water was drained out of each box; the process was repeated as often as necessary. The washing efficiency was tested in a similar manner to that described by Williams *et al.* (1965). It was found that 20 washings were sufficient for the soils under study, so this was the number of washings used at each sampling time for the F_2, H, and mineral horizons. After it was washed, the soil was removed from the sieves of the washing boxes and placed separately in sterile petri dishes containing filter papers and allowed to dry for 24 h. After they were dried, the F_2 needles were cut into 2-mm segments. The F_2 needle fragments and small soil particles were then plated and incubated in the manner described for the L and F_1 needles (100 particles from each horizon at each sampling time).

The results from each soil washing were expressed as the percentage frequency of occurrence of each fungus for each horizon. This figure was arrived at by using the following formula: (number of particles on which fungus occurred)/(total number of particles plated) $\times$ 100.

The actual total number of particles from which fungi were recorded was not always 100. The reasons for this were twofold: (1) a particle was never included in the total if contamination from the air had prevented the recording of fungi from that particle; and (2) a particle was discounted if it had been overgrown by a fungus growing from the other particle on the plate, thus preventing the identification of fungi growing from the overgrown particle.

This method of recording the data allowed the presentation of data on soil fungi in a semiquantitative manner, indicating those fungi most prevalent in the soils at the sampling time.

Samples for soil washing were taken from the study sites at the following times: St. Williams, monthly samples were from April to November, 1966, and from March to June, 1967; Petawawa, a set of samples was received from Petawawa in May, 1967; and Kananaskis, samples were taken at Kananaskis in October, 1967, and May and July, 1968.

(2) Quantitative Studies

The agar film method of Jones and Mollison (1948) was

TABLE 1

Soil pH at study sites

Horizon	St. Williams, *P. strobus*	Kananaskis, *P. contorta*	Petawawa *P. banksiana*	Petawawa *P. resin*; *P. strobus*
H	5.1	6.8	3.9	4.5
A_1	6.5	7.6	4.2	4.6
A_2	6.6	7.6	4.2	4.7
B	—	—	4.6	5.5
C	6.6	7.5	5.5	5.9

used for measuring fungal mycelium in the soils under study. The procedure was as follows.

Soil samples (0.5–10 g, depending on the soil) were ground with a mortar and pestle for 1 min in 15 ml of sterile water, the supernatant was poured into a beaker and the process repeated. A final grinding for 1 min in 20 ml of sterile water was performed and the supernatant decanted off into the beaker. To the resulting 50 ml of supernatant was added 50 ml of hot 2.5% water agar. The soil–agar suspension was mixed and samples removed with a pipette and transferred to the well of a Neubauer haemocytometer slide. A cover slip was placed on the soil–agar mixture and a weight placed on the top to ensure that the film was the correct thickness. After the agar had cooled and set, the film was removed from the haemocytometer and placed on a clean glass slide. The film was allowed to dry on the slide and mounted in glycerine jelly, using a No. 1 glass cover slip. The slides were then ready for observation.

From each soil sample 10 films were prepared. Fifty fields were observed, randomly, from each slide and the mycelium in each film was drawn using a Zeiss camera lucida attached to a Zeiss photomicroscope. The total magnification used was × 645, using phase-contrast illumination, making staining of the agar films unnecessary. The drawings were measured with a map measurer and the measurements converted to meters per gram dry weight of soil.

The sampling times were as follows: St. Williams, samples for quantitative analysis were taken in May, June, August, and September, 1967; Petawawa, samples from Petawawa were received in May, 1967; and Kananaskis, May, 1968.

Results

Qualitative Data

Tables 2–5 give detailed checklists of all the fungi isolated from each or the sites during this study. The data from the intensive study at St. Williams are presented in Table 6, which indicates the seasonal variation and distribution down the profile of all those organisms that occurred at any time with a frequency greater than 10%. Figure 1 is a representation of the data designed to illustrate the succession of fungi down the soil profile. The figure was developed by averaging the frequency of occurrence of each fungus during the sampling period. Only those organisms occurring with an average frequency greater than 5% were included in the final diagram. The results from the three samplings from Kananaskis are shown in Table 7, which shows only those organisms which occurred at least once with a frequency greater than 10%. Figure 2 is a representation of the succession of fungi down the soil profile, derived in the same way as Fig. 1.

The results of the sampling from the two sites at Petawawa are compared in Table 8 with results from a similar sampling time at St. Williams and Kananaskis, again showing only those organisms which occur with a frequency greater than 10%. The succession of fungi down the profiles at the two sites at Petawawa is given in Figs. 3 and 4.

The organism listed in the tables and figures as QL2 is a member of the Sphaeropsidales which has not yet been identified. The codes QL1, QA_2,

TABLE 2

Fungi isolated from soil under *Pinus strobus* at St. Williams

Organism	Soil Horizon						
	L	F_1	F_2	H	A_1	A_2	C
Absidia spinosa Lendner	+	+	+	+	+	+	+
Alternaria spp.	+	+	+		+	+	
Arthrinium sp.	+	+		+	+		
Aspergillus fumigatus Fresenius		+					
A. niger v. Teigh.	+						
Aspergillus spp.		+			+		
Aureobasidium pullulans (de Bary) Arnaud	+	+			+	+	
Beaveria bassiana (Bals.) Vuill.		+					
Cephalosporium spp.	+	+	+	+	+		
Chaetomium spp.	+		+	+	+		
Chrysosporium pannorum (Link) Hughes	+				+		+
Cladosporium herbarum (Pers.) Link.	+	+				+	
Coniothyrium sp.		+			+	+	
Curvularia sp.				+			
Discula sp.		+					
Epicoccum nigrum Link	+	+					
Eurotium sp.			+				
Fusarium solani (Martins) Appel and Wollenweber		+	+	+	+		+

TABLE 2 (*Concluded*)

Organism	Soil Horizon						
	L	F_1	F_2	H	A_1	A_2	C
Fusarium sp. 101	+						
Fusicoccum bacillare Sacc. and Penz	+	+					
Geotrichum spp.					+		
Gliocladium roseum (Link) Thom		+	+	+			
Gliomastix murorum var. *felina* (Marshal) Hughes				+			
Helicoma monospora Kendrick		+					
Melanospora spp.			+	+	+	+	
Mortierella ramanniana var. *angulispora* (Naumov) Linneman						+	
M. vinacea Dixon-Stewart				+	+	+	
Mortierella sp. (*turficola*?)					+	+	
Mortierella sp. 71	+						
Mortierella spp.	+	+	+	+	+	+	
Mucor hiemalis Wehmer	+	+	+	+			
Mucor spp.	+		+	+			+
Nodulisporium sp.	+						
Oidiodendron sp.	+		+	+		+	+
Paecilomyces elegans (Corda) Mason and Hughes		+					
P. farinosus (Dicks ex Fr.) Brown and Smith		+					
P. fumoso-roseus (Wize) Brown and Smith		+		+			
P. variabilis Barron					+	+	
Paecilomyces spp.	+		+				
Penicillium canadense G. Smith	+						
P. citrinum Thom		+	+	+	+		
P. claviforme Bainier	+		+				
P. decumbens Thom						+	
P. frequentans Westling		+	+	+	+	+	
P. janthinellum Biourge				+	+	+	
P. lilacinum Thom				+	+		
P. nigricans (Bain) Thom		+	+	+	+	+	+
P. purpurogenum Stoll		+					
P. restrictum Gilman and Abbott					+	+	
P. thomii Maire		+		+			
Penicillium spp.	+	+	+	+	+	+	+
Periconia macrospinosa Lefebre and A. G. Johnson				+			
Pestalotia sp.	+						
Phialophora spp.	+						
Phoma spp.	+	+	+		+		
Rhizopus sp.		+					
Scopulariopsis sp.		+				+	
Sterile dark QA_2		+	+	+	+	+	+
Sterile dark QL1	+	+					
Sterile dark QL3	+						
Sterile dark mycelia	+	+			+	+	
Sterile hyaline mycelia	+		+				+
Sporonema sp.	+						
Thielevia sp.				+	+		
Torulomyces indicus (Saksena)	+						
T. lagena Delitsch					+	+	+
Trichoderma spp.	+	+	+	+	+	+	
Verticillium terrestre (Link) Landau	+		+	+			
V. lateritum Berkely	+			+	+		
V. sulphurellum Sacc.	+						
Verticillium sp. 48			+	+	+	+	
Verticillium spp.		+	+	+	+	+	
Zygorhynchus moelleri Vuill						+	
α111 (Sphaeropsidales)	+						
QL2 (Sphaeropsidales)	+	+	+				
$QL2_a$ (Sphaeropsidales)	+						

and QA_22 all refer to sterile fungi. QL1 is a green, very slow-growing isolate, while QA_2 and QA_22 are fast-growing, dark olive-green organisms, very similar to each other. Cultures of all the frequently occurring fungi have been kept at the University of Calgary.

Quantitative Data

The measured amounts of fungal mycelium are shown in Tables 9 and 10. Table 9 gives the measured quantities of the mycelium in the soil at St. Williams during the samplings of 1966. Table 10 gives a comparison of the mycelium present in the soils at St. Williams and Petawawa in May, 1967, and at Kananaskis in May, 1968. Figures are expressed in meters of mycelium per gram dry weight of soil.

Discussion

From the data presented in Table 6 it can be seen that, in spite of the marked seasonal changes that occur in the Canadian climate, there are no obvious regular seasonal trends in the qualitative nature of the populations of fungi in the soil under *Pinus strobus* at St. Williams. Although the work of Kendrick and Burges (1963), Gams and Domsch (1969), and Parkinson and Balasooriya (1969) indicated no seasonal cycles in the occurrence of soil fungi, it was felt that this might be due to the lack of climatic extremes in western Europe. In Canadian soils, exposed to great extremes of temperature and moisture, it was felt that marked seasonal fluctuations in fungal populations might have been found.

An examination of Table 6 and Fig. 1 shows that the most frequently occurring fungi in the L layer under *Pinus strobus* were QL1, QL2, and *Alternaria* sp. Associated with these fungi, *Aureobasidium pullulans*, *Fusicoccum bacillare*, *Cladosporium herbarum*, and *Epicoccum nigrum* also occurred frequently. The isolation data for QL1 indicate that this fungus had colonized the leaves

TABLE 3

Fungi isolated from soil under *Pinus resinosa* at Petawawa

Organism	Soil horizon					
	L	F_1	F_2	A_1	A_2	B
Absidia spinosa					+	
Aspergillus nutans McLennan and Ducker						+
Aureobasidium pullulans	+	+				
Cladosporium herbarum	+					
Cylindrocarpon destructans (Zins.) Scholten						+
Gelasinospora sp.				+		
Geotrichum spp.		+				+
Melanospora sp.				+		
Mortierella vinacea						+
Mortierella spp.		+				
Mucor hiemalis			+			
Oidiodendron spp.						+
Paecilomyces elegans		+			+	
P. farinosus	+	+				
Penicillium biforme Thom				+	+	
P. brefeldianum Dodge					+	
P. canadense					+	+
P. frequentans	+	+				
P. nigricans						+
P. thomii		+	+	+		
Penicillium spp.		+	+	+	+	+
Phialophora sp.	+					
Septoria sp.	+					
Sterile brown QLW1	+					
Sterile dark QA_2					+	+
Sterile dark mycelia	+	+			+	
Sterile hyaline mycelia	+				+	+
Tolypocladium sp. α63						+
Trichoderma spp.	+	+	+	+	+	+
Verticillium spp.	+	+				
Zygorhynchus moelleri					+	+
QL2 (Sphaeropsidales)	+					
QL2R (Sphaeropsidales)	+					

before leaf fall in late September; thus in October, just after leaf fall, QL1 occurred with a 90% frequency. This organism did not seem to survive for long once the leaves had fallen, for by November its frequency had dropped to 2.8%.

TABLE 4

Fungi isolated from soil under *Pinus banksiana* at Petawawa

Organism	Soil horizon			
	F	A_1	A_2	B
Absidia spinosa	+			
Aspergillus nutans				+
Emericellopsis sp.		+	+	
Geotrichum sp.		+		+
Mortierella vinacea			+	
Mortierella sp. (*turficola*?)	+	+		
Mucor hiemalis			+	+
Oidiodendron spp.				+
Penicillium biforme		+		+
P. brefeldianum		+	+	
P. frequentans	+	+		+
P. funiculosum Thom	+			
P. nigricans		+		
P. thomii	+			
P. vermiculatum Dangeard			+	+
Penicillium spp.	+	+	+	+
Sterile dark mycelia			+	+
Sterile hyaline mycelia	+	+	+	+
Trichoderma spp.	+	+		+
Zygorhynchus moelleri			+	+
QL2 R (Sphaeropsidales)	+			

In the F_1 horizon under *P. strobus*, QL1, *Fusicoccum bacillare*, and *Auerobasidium pullulans* no longer occurred, whereas *Alternaria* sp., *Cladosporium herbarum*, and QL2 were still found. *Coniothyrium* sp. and *Helicoma monospora* both occurred in the F_1 horizon only. *Helicoma monospora*, which was found in April, 1966, was of interest, as the only other report of this organism is that of Kendrick (1958), who, using damp chambers, isolated it from F_1 layer needles of *Pinus sylvestris* at Delamere forest, England. As this organism grows but slowly on agar plates it is quite possible that its presence is usually masked in plate isolations by the growth of fast-growing fungi such as *Trichoderma*, *Penicillium*, or *Alternaria*. The most prominent feature of the F_1 horizon, however, was the great increase in the frequency of occurrence of species of *Trichoderma* and *Penicillium*, which already formed the major part of the mycoflora.

In the F_2 horizon, species of *Trichoderma* and *Penicillium* occurred with their maximum frequency and together formed the dominant part

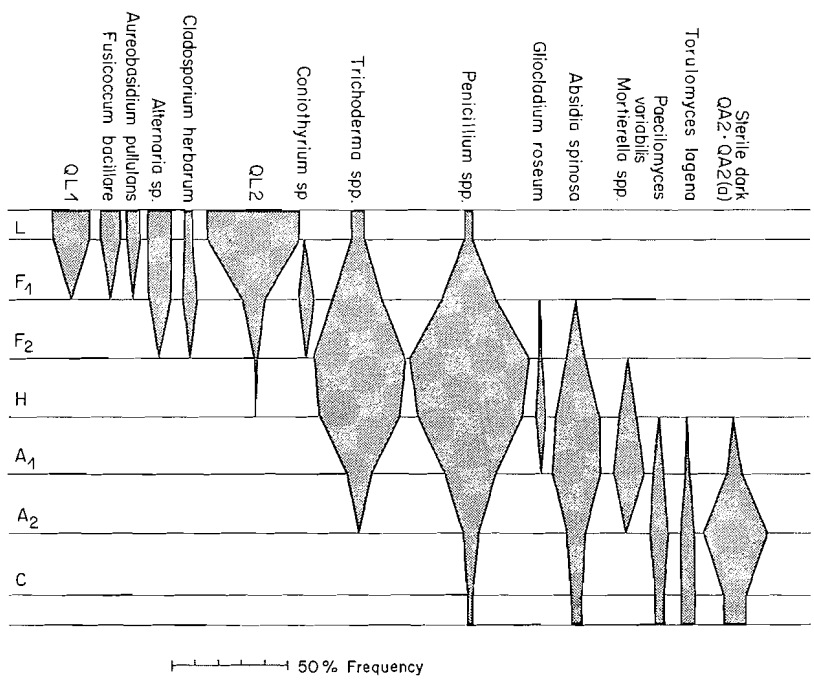

FIG. 1. Distribution of fungi in soil profile under *Pinus strobus* at St. Williams, Ontario.

of the mycoflora, the only other fungus occurring with great frequency being *Absidia spinosa*.

The H horizon was almost the same, with reference to the organisms isolated, as the F_2 horizon, with the exception that species of *Mortierella* occurred there.

The A_1 horizon was rather similar to the H horizon, which was not unexpected as it was

TABLE 5

Fungi isolated from soil under *Pinus contorta* at Kananaskis

Organism	Soil horizon							
	L	F_1	F_2	H	A_1	A_2	B	C
Alternaria spp.	+	+					+	
Arthrinium sp.				+				
Arthrobotrys sp.					+			
Aureobasidium pullulans	+							
Beauveria sp.	+	+	+					
Botrytis cinerea	+							
Cephalosporium spp.			+		+	+	+	
Chaetomium sp.			+	+				
Chrysosporium pannorum					+	+	+	+
Cladosporium herbarum	+	+	+					
Coniothyrium sp.	+	+	+	+		+		
Cylindrocarpon destructans					+	+	+	
Discula sp.	+							
Epicoccum nigrum		+						
Fusarium spp.				+	+			+
Mortierella sp. 71				+	+	+	+	+
Mortierella spp.			+	+				
Mucor circinelloides van Tieghem						+		
M. hiemalis			+	+	+			
Oidiodendron spp.	+						+	
Paecilomyces farinosus		+						
Paecilomyces spp.			+					+
Penicillium canadense		+		+	+	+	+	
P. thomii		+		+	+			
Penicillium spp.	+	+	+	+	+	+	+	+
Pestalotia sp.				+				
Phialophora spp.	+	+					+	
Phoma spp.	+	+	+	+				
Sclerotium sp.					+			
Sporonema sp.		+	+					
Sterile dark mycelia	+	+	+	+	+	+	+	+
Sterile hyaline mycelia	+							
Torulomyces lagena				+				
Trichoderma spp.	+	+	+	+	+	+	+	+
Ulocladium atrum Preuss	+	+	+	+				
Verticillium spp.			+	+	+	+		+
QL2 (Shaeropsidales)	+	+						
α111 (Sphaeropsidales)		+			+			

TABLE 6

Seasonal variation of fungi in soil under *Pinus strobus* at St. Williams. Figures expressed as percentage frequency of occurrence

	1966							1967				
	Apr.	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Mar.	Apr.	May	Jun.	Jul.
L horizon												
QL 2	18.9	6.8	—	23.2	18.8	0	52.8	82.0	81.8	78.0	53.2	2.0
Alternaria sp.	16.4	0	—	24.6	34.8	0	18.1	4.0	0	14.0	8.5	0
QL 1	16.4	5.4	—	2.9	0	89.9	2.8	14.0	16.0	4.0	0	2.0
Cladosporium herbarum	10.7	0	—	5.8	1.4	0	1.4	0	9.1	0	0	0
Epicoccum nigrum	11.5	0	—	0	10.1	0	11.1	12.0	0	6.0	0	2.0

TABLE 6 (*Concluded*)

	1966							1967				
	Apr.	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Mar.	Apr.	May	Jun.	Jul.
Fusicoccum bacillare	0	79.9	—	8.7	0	0	1.4	0	0	0	0	0
Aureobasidium pullulans	0.8	1.4	—	1.6	0	1.3	5.6	24.0	18.2	6.0	2.0	2.0
QL 3	0	0	—	0	0	0	0	0	0	0	19.1	0
Penicillium spp.	0.8	0	—	9.4	15.9	1.3	0	0	0	0	0	0
Trichoderma spp.	0	0	—	1.8	1.4	0	2.8	0	0	0	0	36.0
F_1 horizon												
QL 2	0	0	—	0	0	25.0	8.3	20.0	24.0	3.0	12.0	0
Alternaria sp.	12.8	0	—	10.9	2.0	8.3	23.0	16.0	4.0	3.0	8.0	0
Cladosporium herbarum	24.3	8.0	—	10.9	0	2.1	6.2	6.0	0	0	2.0	0
Penicillium spp.	0	14.0	—	12.5	40.0	6.2	6.2	42.0	48.0	51.5	6.0	26.0
Trichoderma spp.	0	16.0	—	31.3	44.0	37.5	12.5	10.0	8.0	43.5	2.0	72.0
Helicoma monospora	17.6	0	—	0	0	0	0	2.0	0	0	0	0
Coniothyrium sp.	0	0	—	0	0	0	2.1	2.0	0	0	60.0	0
F_2 horizon												
QL 2	—	0	0	0	0	0	0	0	15.5	0	0	0
Penicillium spp.	—	3.8	20.3	21.7	36.3	78.6	74.6	86.0	78.0	59.0	80.0	26.0
Trichoderma spp.	—	32.7	23.4	31.9	14.3	23.8	37.5	66.0	14.5	76.6	56.0	72.0
Absidia spinosa	—	25.0	14.1	21.7	14.3	0	1.5	2.0	14.5	0	4.0	0
Verticillium album	—	0	10.9	0	0	0	0	0	0	0	0	0
Gliocladium roseum	—	0	0	0	0	0	10.4	0	0	2.1	0	0
Mucor hiemalis	—	3.8	0	0	0	0	1.5	0	12.0	0	0	0
H horizon												
Penicillium spp.	46.1	35.1	41.2	21.7	0	—	23.6	62.0	78.0	78.0	78.0	46.0
Trichoderma spp.	34.9	20.8	13.8	34.8	24.2	—	32.0	54.0	8.5	63.4	32.0	80.0
Absidia spinosa	9.4	32.5	13.8	36.2	27.4	—	1.4	20.0	42.5	0	24.0	2.0
Gliocladium roseum	0	0	0	0	0	—	50.0	2.0	0	4.9	0	0
Mortierella vinacea	0	0	0	0	0	—	0	0	49.0	4.9	0	0
Mortierella spp. (other than *vinacea*)	0	0	0	0	34.9	—	0	0	0	0	0	0
Fusarium solani	2.8	1.3	1.1	1.4	0	—	1.4	12.0	0	0	4.0	4.0
Cephalosporium spp.	0	0	0	4.3	0	—	0	0	0	0	28.0	0
A_1 horizon												
Penicillium spp.	38.2	44.2	0	3.1	5.7	—	11.0	16.5	11.0	47.7	63.7	12.0
Trichoderma spp.	10.9	0	2.3	0	5.2	—	5.8	1.1	8.0	20.9	32.5	8.0
Absidia spinosa	22.8	33.1	11.5	28.1	22.8	—	36.1	13.2	8.0	20.9	32.5	8.0
Mortierella vinacea	0	0	27.0	0	0	—	36.6	18.0	32.0	7.0	10.2	2.0
Mortierella spp. (other than *vinacea*)	0	0	0	0	24.7	—	3.5	6.6	2.0	5.8	0	6.0
Sterile dark mycelia (QA_2, QA_22)	0	10.5	8.1	5.2	5.2	—	26.1	40.7	5.0	17.4	7.5	0
Torulomyces lagena	0	0	0	0	2.0	—	5.2	0	6.0	0	0	14.0
Paecilomyces variabilis	0	0	0	0	0	—	0	17.6	9.0	0	1.2	12.0
A_2 horizon												
Penicillium spp.	5.0	0	0	0	12.9	—	10.1	12.0	8.0	13.1	6.0	0
Absidia spinosa	17.1	0.5	4.7	2.1	0	—	7.2	14.0	0	3.6	19.0	4.0
Sterile dark mycelia (QA_2, QA_22)	35.3	24.5	41.2	1.1	10.0	—	44.4	0	24.0	33.1	38.0	43.0
Torulomyces lagena	0	0	0	0	19.7	—	13.5	2.0	3.0	10.7	2.4	13.0
Paecilomyces variabilis	0	0	0	0	7.0	—	1.9	48.0	3.0	16.7	32.4	9.0
Verticillium sp. 1	0	0	12.6	0	3.0	—	0	4.0	0	1.2	13.2	0
Oidiodendron spp.	0	0	0.5	0	0	—	0	0	3.7	0	2.4	4.0
Scopulariopsis sp.	0	0	0	0	0	—	0	0	13.0	0	0	0
C horizon												
Penicillium spp.	—	0.6	1.2	0	22.0	0	2.7	0	—	0	12.0	0
Absidia spinosa	—	0.6	0	0	50.0	0	0	0	—	0	2.0	0
Sterile dark mycelia (QA_2, QA_22)	—	9.4	0	0	0	0	17.2	0	—	36.3	8.0	44.0
Torulomyces lagena	—	0	0	0	16.0	0	22.1	0	—	0	12.0	0
Paecilomyces variabilis	—	0	0	0	0	0	0	4.0	—	0	16.0	22.0
Verticillium sp. 1	—	0	0	0	0	0	0	0	—	0	12.0	0

very organic in nature. However, the incidence of species of *Trichoderma* and *Penicillium* was somewhat lower, whereas that of the Mucorales (*Mortierella*, *Absidia*) appeared to be increased. It is also in the A_1 horizon that the organisms forming the major part of the mycoflora in the lower horizons were first found. These organisms under *Pinus strobus* were *Paecilomyces variabilis*, *Torulomyces lagena*, and sterile dark mycelia.

At St. Williams, *Trichoderma* spp. never occurred below the A_1 horizon, whereas species of *Penicillium* were found at reduced frequencies in both the A_2 and C horizons. *Absidia spinosa*, *Paecilomyces variabilis*, *Torulomyces lagena*, and sterile dark mycelia formed the major portion of the mycoflora in both the A_2 and A horizons.

An examination of Table 7 and Fig. 2 shows that the site at Kananaskis was similar in some ways to that at St. Williams with respect to its mycoflora, though *Fusicoccum bacillare* and QL1 did not occur in the L horizon. The general pattern of an increase in the incidence of *Penicillium* spp. and *Trichoderma* spp. into the F_2 and H horizon was very similar at the two sites, as was the presence of fungi from the Mucorales at both sites. At Kananaskis, however, *Mucor hiemalis* occurred in the H layer and not *Absidia spinosa*.

TABLE 7

Fungi isolated from soil under *Pinus contorta* at Kananaskis. Figures expressed as percentage frequency of occurrence

	Date		
	Oct. 1967	May 1968	July 1968
L horizon			
QL2	36	11	0
Cladosporium herbarum	30	24	18
Sterile dark	4	19	0
Coniothyrium sp.	4	0	9
Aureobasidium pullulans	4	2	12
Penicillium spp.	8	2	0
Trichoderma spp.	0	2	0
F_1 horizon			
QL2	32	4	0
Cladosporium herbarum	8	2	2
Penicillium spp.	36	0	16
Trichoderma spp.	30	28	58
Coniothyrium sp.	16	0	0
Sterile dark	2	14	5
α111 (Sphaeropsidales)	0	22	0
Sporonema sp.	0	16	0
Penicillium thomii	0	0	17
Mucor hiemalis	0	0	2
F_2 horizon			
Trichoderma spp.	56	38	43
Penicillium spp.	48	20	23
Sterile dark	4	2	0
Coniothyrium sp.	2	0	0
Sporonema sp.	4	2	0
Mucor hiemalis	0	2	27
Cladosporium herbarum	0	2	0
Mortierella spp.	0	0	6
H horizon			
Trichoderma spp.	66	26	35
Penicillium spp.	40	12	35
Coniothyrium sp.	2	0	0
Sterile dark	2	2	0
Penicillium canadense	24	0	0
Mucor hiemalis	0	18	29
Mortierella spp.	0	4	4
Penicillium thomii	0	0	41
Verticillium sp.	0	12	0

	Date		
	Oct. 1967	May 1968	July 1968
A_1 horizon			
Trichoderma spp.	—	1	62
Penicillium spp.	—	4	15
Penicillium canadense	—	5	0
Mortierella spp.	—	19	3
Verticillium sp.	—	20	3
Mucor hiemalis	—	7	0
Sterile dark	—	1	7
α111 (Sphaeropsidales)	—	2	0
Chrysosporium pannorum	—	4	1
A_2 horizon			
Sterile dark	33	11	17
Oidiodendron spp.	26	0	0
Chrysosporium pannorum	11	0	15
Penicillium spp.	6	3	6
Mortierella spp.	2	37	17
Penicillium canadense	0	1	0
Trichoderma spp.	0	1	55
Mucor hiemalis	0	3	0
Verticillium sp.	0	4	1
Coniothyrium sp.	0	0	1
B horizon			
Chrysosporium pannorum	55	0	8
Sterile dark	12	6	13
Mortierella spp.	4	16	0
Trichoderma spp.	2	6	12
Penicillium spp.	1	2	1
Penicillium canadense	1	0	0
C horizon			
Chrysosporium pannorum	52	0	0
Mortierella spp.	10	8	0
Sterile dark	20	10	1
Oidiodendron spp.	1	0	0
Penicillium canadense	1	0	0
Penicillium spp.	1	0	0
Trichoderma spp.	2	0	0
α112 (unidentified)	0	12	0

If the fungi occurring in the mineral soil horizons at Kananaskis and St. Williams are compared there appears to be little similarity at all between the two sites, the only thing in common being a reduction in the occurrence of *Penicillium* spp. and *Trichoderma* spp. and the presence of sterile dark mycelia. The fungi of the mineral soils in Kananaskis appear to be *Verticillium* spp., *Chrysosporium pannorum*, and *Oidiodendron* spp.

Although the data given in Table 8, comparing the four sites studied, are based on only one sample from each horizon at one date, some interesting parallels are evident.

(i) In the L layer needles, QL2 occurs frequently at all four sites though, because of the lack of L layer material from the *Pinus banksiana* site at Petawawa, this can only be inferred from its presence in the F layer material from that site.

(ii) In the three sites from which L layer material was obtained, sterile dark mycelia are

TABLE 8

Comparison of four forest sites with respect to the occurrence of microfungi*

Species	*P. resinosus*, Petawawa	*P. banksiana*, Petawawa	*P. strobus*, St. Williams	*P. contorta*, Kananaskis
L horizon				
QL2	14	—	78	11
Sterile dark	41	—	4	19
Alternaria sp.	0	—	14	0
Cladosporium herbarum	3	—	0	24
Penicillium thomii	0	—	0	0
F horizon				
Trichoderma spp.	40	40	60	33
Penicillium spp.	33	35	55	10
Penicillium thomii	34	10	0	0
Sphaeropsidales	15	0	0	22
Sterile dark	3	0	0	12
Sporonema sp.	0	0	0	16
QL2	0	15	0	0
H horizon				
Trichoderma spp.	—	—	63	26
Penicillium spp.	—	—	78	12
Mucor spp.	—	—	0	18
Verticillium sp.	—	—	0	12
A_1 horizon				
Penicillium spp.	100	56	48	4
Trichoderma spp.	78	2	26	1
Sterile dark	0	0	17	7
Emericellopsis sp.	0	24	0	0
Absidia spinosa	—	—	21	0
Verticillium sp.	0	0	0	20
Mortierella spp.	0	0	0	19
A_2 horizon				
Penicillium spp.	75	41	13	3
Trichoderma spp.	50	0	0	1
Sterile dark	0	0	36	11
Mortierella sp.	0	33	0	37
Paecilomyces variabilis	0	0	16	0
Sterile hyaline	0	15	0	0
B horizon				
Cylindrocarpon destructans	47	0	—	—
Aspergillus nutans	32	19	—	—
Zygorhynchus moelleri	1	44	—	—
Penicillium spp.	3	15	—	6
Trichoderma spp.	2	0	—	2
Sterile dark	14	0	—	6
Geotrichum sp.	0	12	—	0
Mortierella sp.	—	—	—	16

*Samples from St. Williams and Petawawa taken May, 1967; samples from Kananaskis taken May, 1968.

frequent in occurrence. At Petawawa and Kananaskis, however, the sterile dark organisms are more frequent than QL2, whereas the reverse is true at St. Williams.

(iii) *Cladosporium herbarum*, which appeared at Kananaskis on the L layer needles, is common to the three study sites from which L layer materials were obtained. Though it did not occur in May,

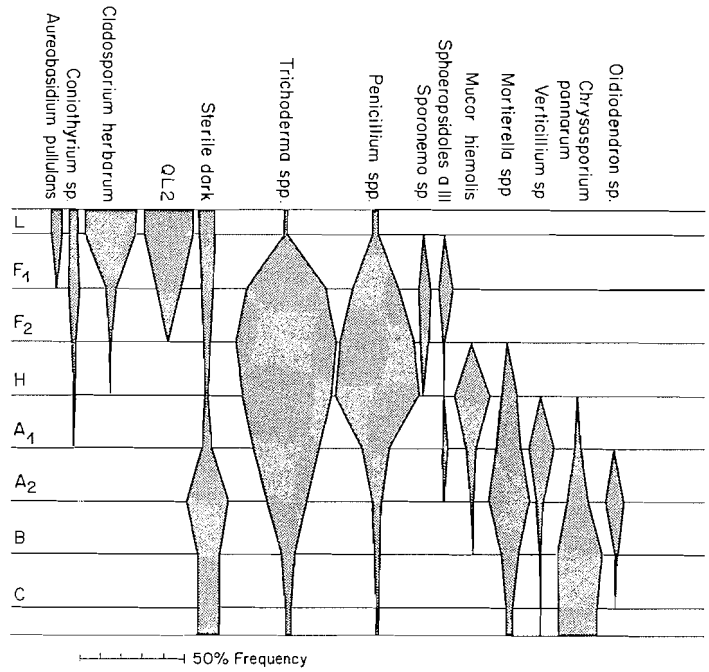

FIG. 2. Distribution of fungi in soil profile under *Pinus contorta* at Kananaskis, Alberta.

TABLE 9

Mycelium in soil at St. Williams, 1966, meters per gram dry weight ± one standard deviation

Horizon	May 27	Jun. 17	Aug. 10	Sept. 9
H	72±16	102±21	302±40	90±16
A_1	15±6	50±8	41±3	16±5
A_2	6±3	11±4	17±4	16±4
C	4±2	5±3	4±1	17±3

TABLE 10

Comparison of mycelium in soil at four sites,* meters per gram dry weight ± one standard deviation

Horizon	*Pinus banksiana*, Petawawa	*Pinus resinosa*, Petawawa	*Pinus strobus*, St. Williams	*Pinus contorta*, Kananaskis
H	—	—	210±25	2699±498
A_1	83±12	184±37	30±5	1540±229
A_2	49±9	31±7	16±4	351±55
B_1	26±4	15±3	—	140±37
B_2	—	—	—	—
C	—	—	18±2	31±13

*Samples from Petawawa and St. Williams taken May, 1967; samples from Kananaskis taken May, 1968.

1966, at St. Williams it was common on the L layer needles from that site later in the year.

(iv) The occurrence of species of *Trichoderma* and *Penicillium* increases from the L to the H layer at all four sites, until in the H layer they are the dominant fungi isolated. At Kananaskis, however, *Mucor hiemalis* and *Verticillium* spp. are also very common in the H layer.

The fungal floras of the mineral soil horizons from the four study sites are much more varied. The A_1 horizons of all sites tend to have *Penicillium* spp. and *Trichoderma* spp. as the dominant

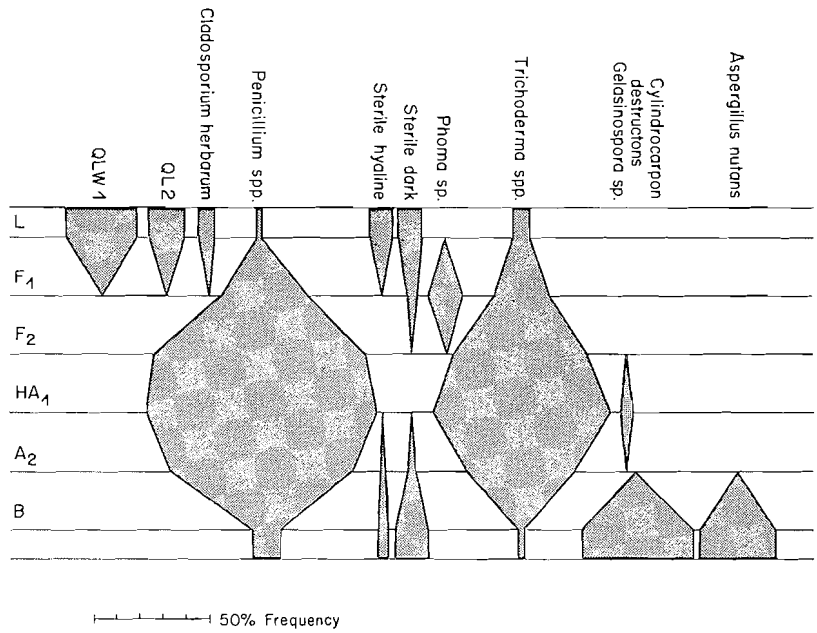

FIG. 3. Distribution of fungi in soil profile under mixed *Pinus strobus* and *P. resinosa* at Petawawa, Ontario.

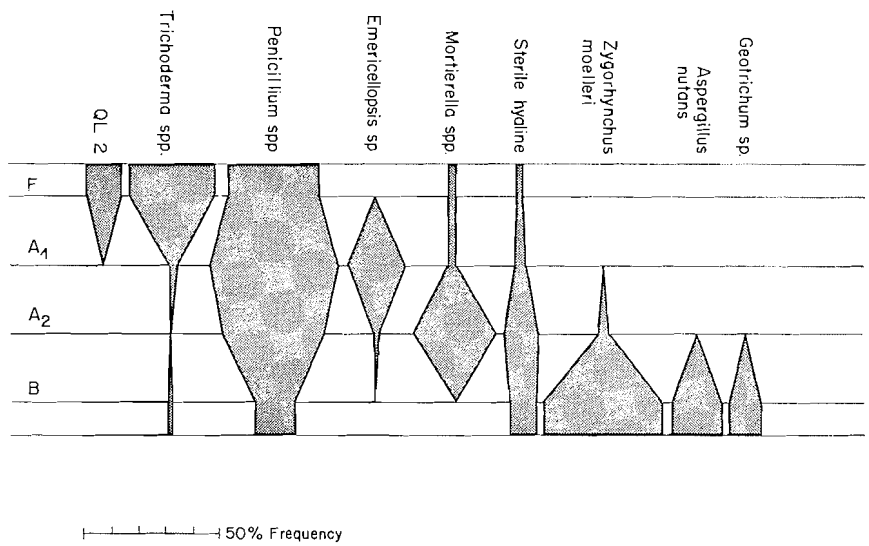

FIG. 4. Distribution of fungi in soil profile under *Pinus banksiana* at Petawawa, Ontario.

fungi, but the fungi associated with them are different in each case. Thus, under *Pinus banksiana* at Petawawa the associated fungus is *Emericellopsis* sp., under *Pinus strobus* at St. Williams they are sterile mycelia and *Absidia spinosa*, and at Kananaskis under *Pinus contorta* they are *Verticillium* spp. and *Mortierella* spp.

In the A_2 and B horizons the mycofloras of the four sites have very little in common, thus: (i) under *Pinus resinosa* and *P. strobus* at Petawawa, species of *Trichoderma* and *Penicillium* are the dominant organisms in the A_2 horizon, while in the B horizon *Cylindrocarpon destructans*, *Aspergillus nutans*, and sterile dark mycelia are the major fungi found; (ii) under *Pinus banksiana* at Petawawa, *Penicillium* spp., *Mortierella* spp., and sterile hyaline mycelia are dominant in the A_2 horizon and *Aspergillus nutans*, *Zygorhynchus moelleri*, *Penicillium* spp., and *Geotrichum* sp. are found in the B horizon; (iii) at St. Williams, under *Pinus strobus*, *Penicillium* sp. and *Paecilomyces variabilis*, and sterile dark mycelia are the most common fungi in the A_2 horizon; and (iv) at Kananaskis under *Pinus contorta*, sterile dark mycelia and *Mortierella* spp. are the most common fungi in the A_2 and B horizons.

In their work on *Pinus sylvestris*, Kendrick and Burges (1963) describe a succession of fungi on the needles, beginning with parasites on the living needles such as *Lophodermium pinastri* and *Coniosporium* sp. These parasites are then followed by weak parasites, such as *Aureobasidium pullulans* and *Fusicoccum bacillare*, which infect the senescent leaves. The final stage in the succession described for *Pinus sylvestris* was an association of basidiomycetes and species of *Penicillium* and *Trichoderma*, which were considered to be present mainly as spores. Hudson (1968) reviewed the ecology of fungi on aboveground remains, and presented a general schema for the colonization of decaying leaves of plants. He proposed a succession, beginning with the colonization of living leaves by parasites, followed by primary saprophytes (essentially the weak parasites of Kendrick and Burges). The primary saprophytes are then followed by secondary saprophytes, consisting of ascomycetes, basidiomycetes, and Fungi Imperfecti. The final stage in Hudson's succession is the "soil inhabitants," under which he included the Mucorales and species of *Trichoderma* and *Penicillium*.

In the present study, living needles were not examined, so no parasites of living pine needles were found, but the group of primary saprophytes was well represented in the litter. Hudson (1968) divides the primary saprophytes into restricted and common primary saprophytes and indicates that *Fusicoccum bacillare* is a primary saprophyte, restricted to *Pinus*, a view supported by the data from St. Williams. Hudson's group of common primary saprophytes contains *Alternaria tenuis*, *Aureobasidium pullulans*, *Botrytis cinerea*, *Cladosporium herbarum*, and *Epicoccum nigrum*, but Hudson states that only *Aureobasidium pullulans* is found on *Pinus*. The data from this study contradict this view, for *Epicoccum nigrum*, *Cladosporium herbarum*, and a species of *Alternaria* (which may have been *A. tenuis*) were found regularly on the needles of *Pinus strobus*. On *Pinus contorta* needles *Epicoccum nigrum* and *Alternaria* sp. were occasionally found and *Cladosporium herbarum* was found in all the *Pinus* species from which L layer material was examined. These data would therefore suggest that, with the exception of *Botrytis cinerea*, which was found very occasionally on *Pinus contorta*, the group of fungi which Hudson lists as common primary saprophytes are well represented on *Pinus* litter.

The organism listed as QL2, which was isolated from the litter of all the *Pinus* species studied, is of some interest for it does not appear to have been isolated from pine litter by other researchers. Its occurrence on the L layer needles and subsequent disappearance below the F_1 layer would indicate that it fits into the category of primary saprophyte. Unpublished studies by the authors on aspen (*Populus tremuloides*) leaves at Petawawa and by Visser (unpublished) on aspen leaves at Kananaskis have shown that this fungus is present on deciduous litter too. It is possible that this fungus occurs only in areas that experience severe winters, for laboratory studies indicate that sporulation only occurs after a prolonged period of low temperatures.

Of the waves of secondary saprophytes described by Hudson, few, if any, were found during the present study. It is possible that *Coniothyrium* sp. and *Sporonema* sp. on *Pinus contorta* and *Coniothyrium* sp. and *Phoma* sp. on *Pinus strobus* litter represented the first wave of secondary saprophytes. The second wave of secondary saprophytes, the basidiomycetes, were not iso-

lated during this study, as a result of the methods used. No special media for isolation of basidiomycetes were used, and therefore the lack of these organisms in this study certainly does not imply their absence. The final stage in Hudson's schema is the presence of "soil inhabitants" on the now partially decomposed materials. Included as soil inhabitants are *Penicillium* spp., Mucorales, and possibly *Trichoderma* spp., all of which are common in the F_2 and H layers of the four areas studied.

From the above discussion it appears that the succession of fungi on the litter of *Pinus* follows roughly the same pattern as the succession of fungi on the litter of most other plant species. In fact, the succession on *Pinus* appears to be far closer to that on other plant species than the studies by Kendrick and Burges (1962), considered in Hudson's review, had suggested. If one takes the view, taken by Garrett (1963), that these successions are regulated mainly by the nature of the carbon substrates available to microorganisms during the decay of plant remains, then it is not surprising that such similarities exist. The details of these successions would, however, be expected to vary according to the conditions under which decomposition was taking place, for fungi with a competitive advantage under one set of environmental conditions may not have that advantage under differing conditions.

As far as the mineral horizons of the soil are concerned, the fungi occurring appear to vary from place to place, though certain fungi can be considered typical of the mineral horizons. Sterile dark mycelia and *Mortierella* spp. appear to occur in most soils studied; *Chrysosporium pannorum*, *Oidiodendron* spp., and *Paecilomyces* spp. seem to be fairly widespread, occurring at Delamere (Williams 1963; Williams and Parkinson 1964), and at both Kananaskis and Petawawa. *Cylindrocarpon destructans* occurs in the mineral soil of some forest soils, having been reported from Freshfield, England, by Parkinson and Balasooriya (1969), as well as at the *Pinus banksiana* site at Petawawa and under *P. contorta* at Kananaskis. *Torulomyces lagena*, on the other hand, appears, so far, to be restricted to soils of North America, having been isolated from peat soils in Ontario (Barron 1961), Wisconsin forest soils (Christensen 1969), and the site at St. Williams, Ontario.

Although it was not possible to demonstrate any clear trends related to seasonal change as far as the species of fungi were concerned, the quantitative studies at St. Williams, performed in 1967, indicated a very clear seasonal trend. The data presented in Table 9 show that there is a marked increase in the fungal mycelium during spring to summer, followed by a sharp decline in the fall. This is quite a different pattern from that shown by Nagel-de-Boois and Jansen (1966), who demonstrated a spring peak and a fall peak. It is possible that these differences are due to the marked seasonal changes that occur in Canada, compared with the milder conditions in Holland.

A feature of the distribution of the fungal mycelium down the soil profiles is the fact that the amount decreases with depth in all of the sites studied (see Table 10); this result agrees well with data of Nagel-de-Boois and Jansen (1966), Nicholas and Parkinson (1967), and Parkinson *et al.* (1968). This decrease with depth has been explained by a decrease in the organic matter content with depth. Nagel-de-Boois and Jansen (1966) have shown that, if the data are expressed as meters per gram of organic matter, then there is a trend for the mycelium to increase with depth, suggesting an increase in efficiency of the organisms living at lower depths. These results are confirmed to some extent by oxygen uptake experiments performed by Parkinson *et al.* (1968), who showed that oxygen uptake per gram of organic matter was high in the L, A_1, and C horizons under *Pinus nigra* but lower in the F_1, F_2, and H horizons of the same soil.

One of the surprising features of the data obtained from the various sites is the great difference in the mycelial lengths, ranging in the A_1 horizon from 83 meters in the jack pine site at Petawawa, to 1540 m/g in the lodgepole site at Kananaskis, a 17-fold difference. Without more data it is difficult to interpret these differences in terms of the respective environments. One possible explanation may be found in the shorter summers found in Alberta, as compared with Petawawa or St. Williams, permitting only a slow breakdown of dead mycelium. To interpret these data accurately, it is really necessary to be able to estimate the growth rate of mycelia in the soil and the decomposition rate, and to be able to distinguish between live and dead mycelium. At the present time this is not possible.

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